Sins of omission and sins of commission: St Thomas Aquinas and the devil

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ABSTRACT

As the largest surviving marsupial carnivore, the Tasmanian devil is an iconic species. A disfiguring and invariably fatal facial cancer, first reported in 1996, has now spread across most of the range of the devil, leading to population declines of up to 90% and a prognosis of likely extinction in 15-20 years. Transmission experiments have confirmed that the cancer is infectious and genetic evidence shows that it is a transmissible cell line. Potential management strategies are limited, but include establishing insurance populations, disease suppression by removal of infected individuals, selection for resistance and developing a vaccine. None of these strategies is guaranteed to be successful. Some, such as establishing free-ranging populations on offshore islands that currently have no devil population, might possibly impact on other threatened species. We evaluate the range of management options and argue that conservation biologists sometimes prefer "sins of omission", failing to take action, with attendant risks, over "sins of commission", taking actions that might backfire.

Key words: Tasmanian devil; *Sarcophilus harrisii;* facial tumour disease; wildlife disease; conservation biology.

Introduction

Thomas Aquinas, in his *Summa Theologica*, written between 1265 and 1274, considers "sins of omission" (failures to do something one should) less serious than "sins of commission" (doing something one should not) (see the English Dominican Province translation of the Summa Theologica, 1920). In this paper, we describe how this distinction from mediaeval theology is influencing the development of conservation strategies for the Tasmanian devil, threatened by an epidemic of an infectious cancer.

Tasmanian devil facial tumour disease (hereafter DFTD) is an invariably lethal cancer of the largest surviving marsupial carnivore, the Tasmanian devil *Sarcophilus harrisi* (see Figure 1).

It is an infectious cell line (Pearse and Swift 2006, Siddle et al. 2007), which arose in a single individual and has since spread clonally across more than 60% of the geographic range of the devil since its first discovery near Mt William in north-east Tasmania (McCallum et al. 2007, McCallum 2008). It is thought to be spread predominantly by biting, although other means of transmission such as susceptible devils scavenging on the carcasses of infected animals have not been ruled out. The disease is specific to the Tasmanian devil. No signs have been found on quolls or other dasyurids. Foreign tumour cells are not rejected by devils, apparently because of their very low genetic diversity in the Major Histocompatibility Complex (MHC), the gene region associated with self and tumour recognition (Siddle et al. 2007), and it is inconceivable that they would not be rejected by another species.

Standard epidemiological theory suggests that a host specific pathogen should not drive its host to extinction, because at some point host density would fall below the threshold necessary for disease maintenance, at which time the disease would disappear (McCallum and Dobson 1995). However, this relies on transmission being dependent on host density. The transmission rate of sexually transmitted diseases depends on the frequency of infected hosts of the population, not their density. They therefore are capable of driving their sole host to extinction (de Castro and Bolker 2005). Much of the biting injuries to Tasmanian devils occur between adults during the mating season (Hamede et al. 2008) and therefore DFTD may behave like a sexually transmitted disease. Further, populations in which the disease has been present for 10 years have declined by up to 90%, with continuing declines and high disease prevalence (McCallum et al. 2009). DFTD therefore poses a substantial extinction risk to the Tasmanian devil.

Potential Management Strategies

The options available to manage any wildlife disease are limited (Wobeser 2002, McCallum and Jones 2006). An effective treatment for DFTD has yet to be developed, but even if it were available, treating affected individuals in the wild is unlikely to be a practical management strategy. Possible management options are therefore restricted to:

1. **Establishing insurance populations.** This strategy involves putting devils in places disease cannot reach or preventing disease from reaching existing devil populations.

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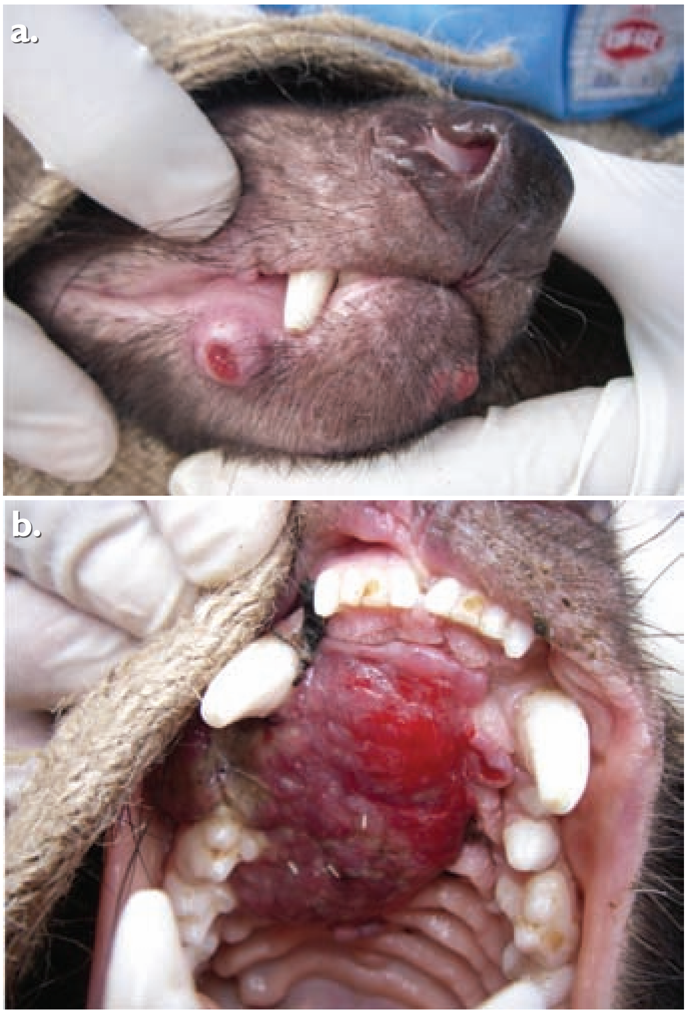

Figure 1: Tasmanian Devil Facial Tumour Disease. a. Early stage tumour on lower lip. b. Late stage tumour on palette. Note fly eggs on tumour surface. c. Late stage tumour. Note displacement of canine tooth. d. Late stage tumour, showing almost total degeneration of the lower jaw.

Photos, R. Hamede

2. **Culling or disease suppression**. This might involve removal of infected animals, removal of particular age or sex classes that are particularly important in disease transmission or conceivably "stamping out" (removal of all individuals within a diseased area).
3. **Genetic management.** This might involve artificial selection for resistance with subsequent introduction of these resistant animals to affected areas, or translocation of resistant genotypes to affected areas. At present, there is no clear evidence that resistant individuals exist in any population, so this strategy remains a long-term option. However, western devil populations (which are still unaffected by the disease) show some differentiation in microsatellites from eastern populations (Jones et al. 2004). If this differentiation also exists at functional loci associated with disease resistance, such as the MHC complex, then it may be that individuals with resistant genotypes exist in some parts of western Tasmania.
4. **Development of a vaccine.** Investigations into the feasibility of developing a vaccine against the tumour are underway (Woods et al. 2007). However, this is a long-term and uncertain option. Even if a vaccine could be developed, producing it in a form that could be delivered (probably orally) to a sufficiently high proportion of the wild population on a broad-scale would be challenging.

The only strategies feasible with existing knowledge are establishing insurance populations and disease suppression. A disease suppression trial is currently underway on the Forestier Peninsula (see Figure 2), which is connected to the mainland of Tasmania by a single bridge across a canal. Preliminary indications are that the removal of all infected individuals from this area that can be captured has had insubstantial effect on the progress of the epidemic (Lachish *et al.*, in press), but it is too early to determine whether this

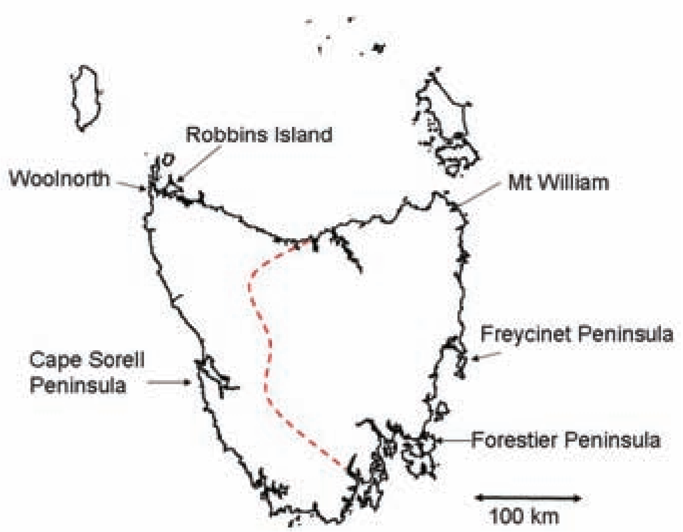

Figure 2: Map of Tasmania showing places referred to in the text, including possible peninsulas to be fenced. The approximate location of the disease front, as of early 2008, is shown as a dashed line

will be an effective strategy. Given the almost complete isolation of the peninsula from mainland Tasmania, if disease suppression is unsuccessful in eradicating the disease here it is unlikely to be successful in more connected populations.

Disease suppression and establishing insurance populations are not entirely disjunct strategies. Even if disease eradication is unsuccessful, a legitimate outcome given the expense of maintaining captive populations (~$12K per devil pa) might be to use disease suppression to maintain a wild, free-ranging population within part of the devil's existing range. Such a population might still be diseased, but ongoing disease suppression could maintain prevalence at a lower level and population density at a higher level than would be the case in an unmanaged diseased population. Experience from the current disease suppression trial on the Forestier Peninsula (Jones et al. 2007) suggests that this might cost about $1.4 K per devil pa. Devils in these populations would be fulfilling their function in the ecosystem and would contribute to maintenance of genetic diversity in the species as a whole. Given that there is no evidence of vertical transmission of the disease and very low prevalence in subadults (McCallum et al. in press) it would be possible to introduce genotypes from such populations into the disease-free insurance population if pouch young were removed and hand raised or there was a generation in a quarantine facility before moving these devils to an insurance population with a lower risk status.

Another essential role for disease suppression is to reduce disease prevalence in a buffer zone outside a fenced enclosure. This has close parallels with the strategy employed in South Africa to control foot and mouth disease, in which a barrier fence around Kruger National Park, (which borders Mozambique and Zimbabwe, where disease is endemic), is linked with vaccination in a buffer zone (Bruckner et al. 2002).

Insurance populations

Establishing insurance populations is currently the only strategy for which we have a high level of confidence of success (McCallum and Jones 2006, McCallum 2008). The primary function of insurance populations is to maintain uninfected devil populations in case disease spreads across the entire range of the devil and causes extinction. If extinction does occur it is likely to be over a timeframe of perhaps 30 years (McCallum et al. 2007), so the insurance population would need to maintain sufficient genetic diversity over this period to enable the reintroduction of devils into areas in which they had become extinct. Given that DFTD is host specific and transmission requires live cells, once devils have become extinct the disease will also disappear. A second function of free ranging insurance populations within the current range of the devil is that they would maintain the ecological role of the devil over at least part of its former range and would prevent it from being listed as extinct in the wild.

Since this paper was written, the IUCN Conservation Breeding Specialist Group has held a workshop in Hobart into developing an insurance strategy for the Tasmanian devil (CBSG 2008). That workshop reached a consensus broadly in line with the opinions we have expressed in this current paper.

"Insurance populations" encompass a range of possibilities, including closely managed captive populations, free ranging populations on islands off the coast of Tasmania and fenced populations either on the mainland of Australia or in Tasmania. Each of these has a range of advantages and disadvantages, summarised in Table 1 and discussed in more detail below.

Closely managed captive populations.

The principal advantage of closely managed captive populations is that, in principle, it is possible to control which females mate with which males. Using standard protocols for captive breeding, it should be possible to minimise loss of genetic diversity over a number of captive generations. Provided captive populations are established with disease-free founders, those on the mainland of Australia or overseas should have virtually no probability of acquiring DFTD. Captive populations within Tasmania will inevitably have a higher probably of acquiring DFTD as it is likely that there will be diseased animals in the wild in close proximity. To date, there have been only two confirmed cases of DFTD acquired whilst animals have been in captivity. These two cases, in a single wildlife park, are likely to have arisen because of a breakdown in biosecurity.

As the sole component of the insurance population, closely managed populations have several disadvantages. First, although Tasmanian devils have been successfully bred over a number of years in some Tasmanian wildlife parks, reproductive success in captivity is generally quite low. Although matings may be planned to maximise retention of genetic diversity, unless all are equally successful, there is certainly the potential for selection to occur. Traits that maximise reproductive success in captivity may well not be desirable in animals when they are reintroduced to the

Table 1. Issues associated with different types of potential insurance populations

	Captive populations (national & international)	Islands	Fenced reserves Mainland Australia	Undiseased Tasmanian peninsulas	Diseased Tasmanian peninsulas
Number of sites	10–40	1-6	1-2	3	3
Number of devils per site (total)	4-12 (<1,000)	~100	50-100	100-300	100-300
Effective to actual population size ratio (Ne/N) (Jones et al 2007)	Higher (0.3)	Lower (0.1)	Lower (0.1)	Lower (0.1)	Lower (0.1)
Ecological impacts of devils on conservation value of area for fauna at risk from foxes in Tasmania	No	Perhaps	No	Perhaps	Perhaps
Retention of wild adaptations (natural behaviours) and parasite communities	No	Yes	Yes	Yes	Yes
Ecological functionality	No	Perhaps (overabundant grazers on some islands)	No	Yes	Yes
Biosecurity risk (natural or sabotage)	Low (higher in Tasmania)	Low (moderate for sabotage)	Low	High	High
Disease eradication necessary (not including incursions)?	No	No	No	In buffer zone	Yes
Cost of establishment	High	Low	High	Medium	High
Cost of managing	High	Low	Medium	Medium	Medium
Stakeholders & land tenure	Many	Varied	Land purchase required	Varied; compensate livestock losses?	Varied; compensate livestock losses?
Time scale for implementation	Short (already in place)	Short – medium (requires impact assessment, stakeholder negotiations)	Medium-Long (Sites to be identified, feasibility and logistics need investigation)	Medium-long (Sites to be identified, feasibility and logistics need investigation)	Trial underway; too early to assess likely success

wild. Tasmanian devils reproduce a limited number of times (females usually first breed at two years of age and generally senesce beyond four years of age Guiler 1978, Pemberton 1990, Jones et al. 2008). This means that two or three poor breeding years may jeopardise the survival of a breeding colony. There may also be losses of natural behaviour and there will certainly be losses of parasites and commensal fauna. As a source of animals to be reintroduced to the wild, there is increasing evidence that captive reared animals do not perform as well as translocated wild caught animals (Jule et al. 2008). Finally, closely managed captive populations do not perform any ecological role and their maintenance would not prevent devils from being listed as extinct in the wild.

Substantial progress has been made in establishing a closely managed captive population. The first intake of 26 founders, when more than two years of age, were sent to the mainland between December 2006 and January 2007, after a quarantine period in Tasmania. Their reproductive success was limited in the majority of breeding groups in the first year, although it was somewhat better in the 2008 breeding season. In early 2007, 31 disease-free Tasmanian devils were wild-caught at weaning age and most were sent to four mainland Australian zoos, under the Aegis of ARAZPA (the Australasian Regional Association of Zoological Parks and Aquaria). A further 60 individuals one-year-old individuals were caught from the disease-free West Coast early in 2008 and most were transferred to mainland zoos in December 2008.

Fenced enclosures on the Australian mainland.

The IUCN CBSG workshop (CBSG 2008) reached a strong consensus that it was important to explore the possibility of free ranging extensive enclosures as an important component of the insurance population. Conventional prescriptions for the maintenance of genetic diversity within a population suggest that an effective population size of at least 500 should be maintained, which corresponds to a census population size of 1500 individuals if matings can be managed and closer to 5000 individuals without management of matings. It was immediately clear that such numbers are beyond the capacity of conventional intensive management and therefore some more extensive management would be

necessary to achieve this goal. The suggestion is that such enclosures, probably several hectares in area, would contain a number of Tasmanian Devils of both sexes, which would need to be supplementary fed, but would otherwise be maintained in a naturalistic setting without intensive management of matings. Whilst we agree that this is an important management option to explore, whether Tasmanian Devils, which are solitary animals, will successfully breed at densities an order of magnitude above those found in the wild is unclear.

Large fenced enclosures on the mainland of Australia should have similar high levels of biosecurity as closely managed captive populations. In principle, they may be able to maintain natural behaviours better than closely managed captive populations. However, maintaining multiple males and females together at high density in captive situations results in very low breeding success. Natural devil densities are of the order of 1-2 individuals km^{-2} (McCallum et al. 2007) and thus to maintain a reasonable number of animals at natural densities would require a very large enclosure (at least 50 km^2) with very substantial costs for fence construction and maintenance. Given that matings could not be controlled, the ratio of census to effective population size would be significantly larger than would be the case in closely managed captive populations. Whether such devils would be fulfilling any natural ecological role is debatable. Devils did exist on the mainland before the arrival of the dingo, perhaps as recently as 400 years before present (Archer and Baynes 1973) although this date is disputed (Brown 2006). There is some evidence that devils contribute to suppressing feral predator populations in Tasmania (Jones et al. 2007), a function they could again fulfil if reintroduced to the Australian mainland. However, a proposal to reintroduce devils to mainland Australia outside secure fenced enclosures should probably best be described as "courageous".

Fenced enclosures in Tasmania.

Most of the issues associated with fenced enclosures on the mainland would also apply to fenced enclosures in Tasmania. However, there are two key differences. First, any fenced population in Tasmania would be subject to substantial risks of disease incursion. Maintaining long fences in rugged, forested country with high wombat populations would be extremely difficult. Further, fencing to prevent incursion by disease is more difficult than fencing to prevent predator incursion. The latent period of DFTD is currently unknown, but it is likely to be lengthy. Whereas incursion of a predator into a predator-free area can be detected almost immediately, enclosures in Tasmania would have devils on both sides of the fence and incursion of a diseased animal would only be detected some time after it had occurred. It is highly likely that secondary transmission would occur before such an animal could be removed.

There is one major advantage of fenced enclosures in Tasmania. If they are established in currently undiseased areas, then they have the potential both to maintain devils *in situ* and also to maintain the ecological role of the species in the area.

It is likely that the most feasible option for fenced enclosures in Tasmania would be to attempt to isolate devil populations on peninsulas. Figure 2 shows two potential such sites: the Woolnorth and Cape Sorell Peninsula, both in the Western, currently uninfected, part of Tasmania. In addition, Robbins Island (see Fig 2) has an uninfected devil population. Whilst devils can move to and from the island at low tide, it might be possible to construct a fence or other barrier to isolate the island from the mainland.

The principal challenges in fencing disease-free populations are financial, technical and social. Fences would need to be double and those on peninsulas would need to run into the sea on each side and have secure gates. Fenced enclosures in contiguous habitat would have both greater costs and higher biosecurity risks than peninsulas, because of the need to have barriers against incursion of diseased devils on all sides. There would also be the potential for concern from landholders and other stakeholders. If there were only a few fenced disease-free devil populations, landholders could be concerned that devil management issues might impinge on their land management practices.

There are few peninsulas in Tasmania that are currently uninfected which potentially could be fenced, perhaps 3 at most. Each of these would hold between 100 and 300 devils. The remaining suitable sites that could feasibly be fenced already have disease. These include the Forestier peninsula, which has the highest degree of site isolation and the Freycinet peninsula, which would require only 5 km of fencing. Disease suppression followed by isolation is an option worth exploring at these sites.

Island populations

Introduction of generalist predators to offshore islands has frequently produced substantial conservation problems (Courchamp et al. 2003), although in all such cases the prey species affected have had no evolutionary exposure to the particular predator (especially cats, Salo et al. 2007). The islands being proposed for Tasmanian Devil translocation hold no prey species that do not coexist with devils on the main island of Tasmania. Many of these islands would have supported devil populations for varying periods over the past 13,000 years following sea level rise and the creation of the Bass Strait, with extinction of devils on all but the largest of the islands well before European settlement (Hope 1972). Nevertheless, the proposal has raised some concerns, particularly as IUCN guidelines suggest extreme caution in introducing species to any area outside their natural range (IUCN 1987).

Translocating Tasmanian devils to offshore islands invokes the *Australian Environment Protection and Biodiversity Conservation Act* (1999) and raises some interesting legal dilemmas. The Act requires an environmental risk assessment to be taken for any action that may negatively impact on threatened species or communities or a range of listed marine or migratory species. All offshore islands of Tasmania that potentially might be suitable for devils hold a range of such species. The clear presumption of the Act is that the "actions" to be assessed have the potential only for negative consequences for biodiversity. How the Act should most appropriately be applied when the proposed action is being undertaken for a biodiversity benefit to one species, with potentially negative implications for some other species,

is uncertain. Are all endangered species equivalent in terms of conservation value? In our opinion, an action is justifiable from a biodiversity conservation point of view if its benefit to biodiversity conservation of one species exceeds the risk to other species. In the case of the Tasmanian Devil, failure to establish disease-free populations has an unacceptable risk of leading to extinction of the species in the wild. Unless there was a demonstrable risk of extinction of some other threatened species as a result of Devil introduction to an island, then the action would be justifiable.

A further limitation of the Act is that it is solely concerned with assessing the risk of actions to biodiversity. It does not assess the risk of failure to act. This distinction, of course, has strong parallels with the distinction between sins of omission and sins of commission made by Aquinas. Whether mediaeval theology should be used as a guide to 21st-century biodiversity conservation is doubtful.

Discussion

It should be clear that no single insurance option will satisfy all the requirements of a comprehensive insurance strategy. Each option has its own advantages and disadvantages, benefits and risks. What is required is a portfolio of insurance options. It is also clear that there is limited time in which to act. Unless genetic differences between the eastern and northwestern parts of the devil's range (Jones et al. 2004) do confer resistance to DFTD, it is likely that the disease will be state-wide within 5 years (McCallum et al 2007).

Wider lessons for conservation biology

Whilst this is a unique disease threatening an unusual species, there are some clear lessons for decision-making in conservation biology arising from this case study (Lunney *et al.* 2009, McCallum 2008). Decision-making under uncertainty has recently attracted a lot of research interest (Burgman 2005) mostly from the perspective of making "optimal" decisions, where the objective function to be minimised may be either the cost for a given conservation outcome or the probability of extinction over some given time horizon. Democratically elected governments, however, may in fact be attempting to minimise the probability or extent of negative publicity. In this context, taking an action that turns out to have negative conservation consequences may be a more serious cost than failing to take action, with resulting negative consequences, even if they are greater in magnitude than those resulting from taking action. The response of the politician if no action has been taken would be along the lines of "… it went extinct, but it was a natural event…" . There is no reason why this could not be handled with a standard decision analysis framework, simply changing the objective function to "negative publicity" although quantifying costs in a sensible fashion will be even more difficult than with a standard decision analysis. How, for example, should negative publicity from an extinction following inaction be weighted relative to negative publicity following a failed intervention?

There is, however, an alternative paradigm that may be applicable in many conservation contexts, including this one. This is robust decision-making, which attempts to make decisions that are "good enough" rather than optimal (Regan et al. 2005, Groves and Lempert 2007). Robust strategies perform relatively well compared with alternatives across a broad range of plausible future states: "good enough" means that they should produce acceptable outcomes over the range of plausible states of nature, rather than the best possible outcome given the most likely state of nature. They are also strategies that are adaptable in the light of future information. In the context of the Tasmanian Devil, disease-induced extinction across the current geographic range of the species is unfortunately a plausible future state and therefore a management strategy must be robust to this possible outcome. Given the difficulties associated with captive rearing of the species and the known difficulties with reintroduction of captive reared individuals to the wild, an insurance strategy that relies entirely on captive reared individuals cannot be considered robust. Similarly, relying on fences as a barrier against disease incursion, even if supported by disease suppression, cannot be considered robust to plausible future outcomes.

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APPENDIX

Late stage pouch young attached to teats in the pouch of the mother in a sack. These fully furred young with eyes open will temporarily leave the pouch when the mother is in the den and will permanently emerge within weeks.

Photo: Rodrigo Hamede

APPENDIX I

Battle-scarred adult male wild devil just released from a trap.

Photo: Rodrigo Hamede

Examining inside the mouth of a wild devil for tumours.

Photo: Rodrigo Hamede

Releasing a wild devil from a trap.

Photo: Rodrigo Hamede

When checking traps during the day, devils are usually found curled up asleep.

Photo: Rodrigo Hamede